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SUMMARY

The European slave-making ant *Harpagoxenus sublaevis* has an unusual female polymorphism. In addition to ordinary workers, there are two kinds of reproductive females, the very rare full queens and the much more common ergatoid (*i. e.* workerlike) queens. A genetic mechanism is responsible for the development of larvae into either ergatoid or full queens.

Sixty-one colonies of the closely related North American species *Harpagoxenus canadensis* were collected from several localities in the provinces of Ontario and Quebec, Canada, and a total of 241 workers, 30 intermorphs, and 26 dealate full queens were dissected in order to discover whether a similar polymorphism occurs in this species. However, *H. canadensis* was found to have an essentialy normal polymorphism. All the fecundated reproductive females that we found were dealate full queens. A spermatheca, which constitutes the only significant difference between ergatoid queens and workers in *H. sublaevis,* is absent in all workers and intermorphs of *H. canadensis.*

In addition, we found that colonies of *H. canadensis* are monogynous (like *H. sublaevis*). However, a minority of workers and intermorphs lay eggs even in queen-right colonies. The average number of ovarioles is much lower in *H. canadensis* workers than in those of *H. sublaevis;* but, in both species, it varies over about the same range (table IV). In this respect, *H. canadensis* workers resemble more closely the workers of the host species. The number of Malpighian tubules is five in both the reproductive females and workers. The poison gland is about the same size in both *Harpagoxenus* species, but the Dufour's gland in *H. canadensis* is considerably smaller than in *H. sublaevis.* Thus, in several respects, *H. canadensis* bears a closer resemblance to the common host genus *Leptothorax* (subgenus *Mychothorax*) than *H. sublaevis* does.

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ZUSAMMENFASSUNG

Zum Kastenpolymorphismus von *Harpagoxenus canadensis* M. R. Smith.

Die europäische, sklavenhaltende Ameise *Harpagoxenus sublaevis* weist einen speziellen Polymorphismus im weiblichen Geschlecht auf : Neben normalen Arbeiterinnen kommen zwei Formen von Königinnen vor, das normale, jedoch sehr seltene, geflügelte Weibchen und das viel häufigere arbeiterinähnliche, sogenannte ergatoide Weibchen. Für die Entwicklung von Larven entweder zu ergatoiden oder zu geflügelten Weibchen ist ein genetischer Mechanismus verantwortlich.

Wir sammelten 61 Völker des nahe verwandten, nordamerikanischen *Harpagoxenus canadensis* an verschiedenen Orten in Ontario und Quebec, Kanada, und sezierten daraus insgesamt 241 Arbeiterinnen, 30 Intermorphe und 26 entflügelte Weibchen um festzustellen, ob ein ähnlicher Polymorphismus auch bei dieser Art vorliegt. *H. canadensis* hat jedoch einen recht normalen Polymorphismus. Alle Königinnen, die wir fanden, waren entflügelte Weibchen. Das receptaculum seminis, das den einzig bedeutsamen Unterschied zwischen ergatoiden Weibchen und Arbeiterinnen von *H. sublaevis* darstellt, fehlt allen Arbeiterinnen und Intermorphen von *H. canadensis.*

Weitere Ergebnisse unserer Untersuchung sind folgende : *H. canadensis* ist, wie *H. sublaevis,* monogyn. In wenigen Kolonien legen einige Arbeiterinnen und Intermorphe Eier, auch in weiselrichtigen Völkern. Die durchschnittliche Ovariolenzahl ist bei *H. canadensis*-Arbeiterinnen wesentlich geringer als bei *H. sublaevis,* variiert bei beiden Arten jedoch in etwa demselben Ausmaß (table IV); *H. canadensis*-Arbeiterinnen sind darin den Arbeiterinnen der Wirtsarten ähnlicher. Die Anzahl der Malpighigefäße beträgt 5 bei Weibchen und Arbeiterinnen. Die Giftdrüse hat bei beiden *Harpagoxenus*-Arten etwa dieselbe Größe. Dagegen ist bei *H. canadensis* die Dufour-Drüse erheblich kleiner als bei *H. sublaevis. H. canadensis* ist damit in einer Reihe von Merkmalen der gemeinsamen Wirtsgattung *Leptothorax* (S. G. *Mychothorax*) ähnlicher als *H. sublaevis.*

INTRODUCTION

The genus *Harpagoxenus* consists of four known species : the widespread European *H. sublaevis* (Nyl.), *H. zaisanicus* Pisarski from Mongolia, *H. canadensis* M. R. Smith from eastern Canada and the northern United States, and *H. americanus* (Emery) from southeastern Canada and the eastern and central United States. The first three species share many morphological characters; and they all enslave different species of the genus *Leptothorax,* subgenus *Mychothorax* Ruzsky. *H. americanus* is morphologically dissimilar to the other

species in several respects and parasitizes hosts of the genus *Leptothorax* in the strict sense (or subgenus *Myrafant* M. R. Smith).

It has long been known that the usual queen in *H. sublaevis* is an ergatoid (*i. e.* workerlike) female (ADLERZ, 1896; VIEHMEYER, 1912, 1921; BUSCHINGER and WINTER, 1978). The full, initially winged, queen caste exists in *H. sublaevis;* but it is extremely rare. The development of female larvae into ergatoid or alate females is controlled by a genetic mechanism (BUSCHINGER, 1975, 1978). However, the only character that reliably distinguishes workers from ergatoid queens is the presence of a spermatheca near the ovary of the latter.

The occurrence of ergatoid individuals in *H. canadensis* has also been noted. SMITH (1939) described the « simple ergatoid female », the « intermediate ergatoid female », and the full queen. GREGG (1945) also recorded the occurence of 6 ergatoids and 10 workers in a colony with a normal queen. Finally, CREIGHTON (1950, p. 281) noted concerning *H. canadensis* that « like *sublaevis* it produces ergatoid females in considerable numbers. » However, these authors considered external morphology only and offered no evidence for the existence of fecundated, egg-laying ergatoid females in this species. Thus, we set out to discover whether such ergatoid queens really do occur in *H. canadensis* and, if so, to compare their frequency with that of full queens.

MATERIALS AND METHODS

Colonies of *Harpagoxenus canadensis* were collected in May, June, and July, 1977, at several sites near Rouyn-Noranda, Quebec and in eastern Ontario, Canada. The localities and dates of collection are given in detail in table I. Nests were found in decaying tree stumps and in dead branches lying on the ground. Colonies of *H. canadensis* and its hosts seemed to be especially abundant in areas where jackpine *(Pinus banksiana)* was common. Either in the field or after transferring complete branches or the inhabited parts of stumps to the laboratory, the nest chambers were opened with a knife; and the ants were removed with an aspirator. Since colonies were often rather diffusely distributed in relatively large pieces of wood, they were not always completely collected. Whenever we suspected that a significant part of a colony had been lost, the sample in Table I is marked as being incomplete.

The numbers of adult *Harpagoxenus* workers and young sexuals, host workers, and *Harpagoxenus* pupae were either counted or estimated. Colonies with many pupae were kept alive for several weeks so that we could study the emerging callows.

We dissected a representative sample of old and young *Harpagoxenus* workers, some alate and dealate queens, and all « intermorphs » (individuals that are morphologically intermediate between the ordinary worker and the full queen). Most intermorphs have from 1 to 3 ocelli on the head. In addition, some of the thoracic sutures characteristic of the full queen are more or less

TABLE I. — Census data for 61 colonies of *Harpagoxenus canadensis* from different localities in Ontario and Quebec.
TABELLE I. — Sammeldaten von 61 Völkern von *Harpagoxenus canadensis* aus verschiedenen Vorkommen in Ontario und Quebec.

Colony No.	Locality	Date of collection	*Harpagoxenus canadensis*				Host workers	Remarks
			Queens	♀♀ and intermorphs	♂ -, ♀ -, ♀ - pupae alate	♂♂, ♀♀		
1	Rouyn-Noranda	May 1977	1 d (1)	ca.10 (2)	♂ -, ♀ - p (3)	—	ca. 20	—
2	»	»	1 d	ca.10	♂ -, ♀ - p	—	ca. 70	—
3	»	»	1 d	ca.20	♀ - p	—	ca. 80	—
4	»	»	1 d	ca.15	♂ -, ♀ - p	—	ca. 10	—
5	»	»	1 d	ca.20	♀ - p	—	ca. 90	—
6	»	»	1 d	ca.12	♀ - p	—	ca. 60	—
7	»	»	1 d	6	♀ - p	—	5	—
8	»	»	—	ca.20	♀ - p	—	ca. 50	incomplete ?
9	»	»	1 d	ca.10	♀ - p	—	ca. 20	—
10	»	»	1 d	ca.30	♀ - p	—	ca. 30	—
11	»	»	1 d	ca.15	♀ - p	—	ca. 15	—
12	»	»	1 d	6	♂ -, ♀ - p	—	ca. 20	—
13	»	»	—	3	—	—	—	incomplete
14	»	»	—	10	—	—	ca. 20	incomplete
15	»	»	1 d	—	—	—	5	incipient colony
16	»	»	1 d	41	♂ -, ♀ - p	—	ca. 10	—
17	»	»	—	4	—	—	—	incomplete
18	»	»	—	7	♀ - p	—	2	incomplete
19	»	»	—	1	—	—	2	incomplete
20	»	»	1 d	10	♂ -, ♀ -, ♀ - p	—	ca. 60	—
21	»	»	—	35	—	—	5	incomplete
22	»	»	—	1	♂ - p	—	ca. 30	incomplete
23	»	»	1 d	12	♂ - p	—	5	—
24	»	»	—	49	♀ -, ♀ - p	—	ca. 40	—
25	»	»	—	4	♀ -, ♀ - p	—	5	—
26	»	»	1 d	ca.30	♂ -, ♀ - p	—	ca. 50	—
27	»	»	1 d	1	♂ - p	—	ca. 40	—
28	»	»	1 d	41	♀ - p	—	21	—
29	»	»	1 d	—	—	—	8	incip. col., 5 slave ♀ - p
30	»	»	—	8	♀ - p	—	10	incomplete

31	»	»	1 d		9	♂ -, ♀ -,	☿ - p	—		27	—
32	»	»	—		23	♂ -, ♀ -,	☿ - p	—		30	—
33	»	»	—		32	♀ -,	☿ - p	—		33	—
34	»	»	1 d		20		☿ - p	—		14	—
35	»	»	1 d		20	♂ -, ♀ -,	☿ - p	—		87	—
36	»	»	1 d		3	♂ -, ♀ -,	☿ - p	—		20	
37	Rouyn-	8-11 july	1 d		m (4)	♀ -,	☿ - p	♂♂ ♀♀		m	—
38	Farm-	1977	—		3		☿ - p	♂♂		s (4)	incomplete
39	borough	»	3 d	(1 fertile, 2 not insem.)	m		☿ - p	—		m	slave ♂♂ and ♀♀ (5)
40	»	»	1 d		m		☿ - p	♀♀		m	—
41	»	»	1 d		32	5	☿ - p	10 ♂♂ 27 ♀♀		63	—
42	»	»	1 d		1	—		—		1	incipient colony
43	»	»	1 d		4	—		—		10	incipient colony
44	»	»	1 d		—	5	☿ - p	—		6	incipient colony
45	»	»	—		1	—		—		—	1 larva, incomplete
46	»	»	1 d		3	—		—		ca. 60	young colony
47	»	»	1 d		31	4	☿ - p	3 ♂♂ 4♀♀		41	—
48	»	»	1 d		28	8	☿ - p	8 ♂♂		95	—
49	»	»	1 d		20	10	☿ - p	28 ♀♀		97	—
50	»	»	1 d	(not insem.)	m		☿ - p	♂♂ ♀♀		m	incomplete ?
51	»	»	1 d		l (4)		☿ - p	♂♂ ♀♀		l	—
52	Reneault	»	1 d		2	♂ - p		40 ♂♂		m	—
53	»	»	—		s		☿ - p	♂♂ ♀♀		s	incomplete ?
54	»	»	1 d		m		☿ - p	♂♂ ♀♀		m	—
55	»	»	3 d	(not insem.)	m		☿ - p	—		m	slave ♂♂ and ♀♀ (5)
56	»	»	1 d		s		☿ - p	—		s	slave ♀♀ (5)
57	»	»	1 d		s		☿ - p	—		s	—
58	La Sarre	»	—		l		☿ - p	—		24	incomplete
59	»	»	—		2	—		—		—	incomplete
60	Algonquin	18 june 1977	1 d		m	♂ -, ♀ -,	☿ - p	♂♂ ♀♀		m	—
61	Park	»	—		m	♂ -, ♀ -,	☿ - p	♂♂ ♀♀		m	incomplete

(1) Means a normal, deleate and apparently fertile queen.
(2) ca. means that the numbers were estimated.
(3) Numbers of sexual and worker pupae were not recorded since these numbers change considerably during the breeding season. We only noted whether they were present or not.
(4) s = small, not more than 10 *H. canadensis* ☿☿ and slaves; m = medium, 10-20 *H. canadensis* ☿☿ and 20-60 slaves; l = large, more than 20 *H. canadensis* ☿☿ and 60 slaves.
(5) Slave ♂♂ and/or ♀♀ present in the colony. Such individuals are probably derived from pupae kidnapped during raids.

developed. Occasionally, one or two pairs of vestigial wings are visible. Most of the intermophs appear to correspond to the « simple ergatoid female » of M. R. SMITH (1939). Thus, if one regards only external morphology, *H. canadensis* resembles *H. sublaevis* in that one sees a nearly continuous transition from the simple worker to the alate female (BUSCHINGER and WINTER, 1975).

Dissections were made under water in a small petri dish, the bottom of which was coated with a thick layer of black wax. The petri dish was placed on the stage of a dissecting microscope; and magnifications of 25 × or 50 × were used. An etherized individual was grasped by the petiole with one pair of watch-maker's forceps (Dumont, N°. 5), while a second pair of similar forceps was employed to drag away

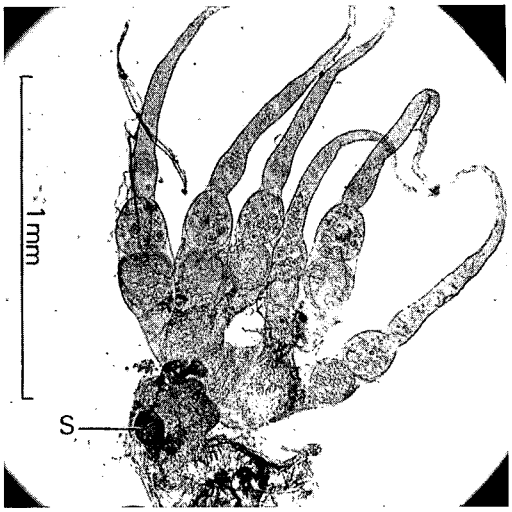

FIG. 1. — Ovary of a young, fertilized female of Harpagoxenus canadensis. *S* : spermatheca.

ABB. 1. — Ovar eines jungen, begatteten Harpagoxenus canadensis - Weibchens. *S* : Spermathek.

the subgenital plate or the whole last segment. In this way, the hind gut, poison gland, Dufour's gland, and the reproductive system could usually be removed. To discover whether a spermatheca was present and, if so, whether it contained sperm, the entire set of organs was placed in a droplet of water on a microscope slide, covered and slightly pressed with a cover glass, and examined under a compound microscope. In addition to the presence or absence of a full or empty spermatheca, we recorded the number and approximate size of the ovarioles and whether or not they contained developing eggs and corpora lutea in their bases (fig. 1).

RESULTS

Table I shows the collection data and the estimated or counted composition of the 61 colonies of *H. canadensis* investigated. Forty (or 2/3) of the samples contained one dealate fertile full queen. Thirty-one colonies produced young alate queens. Since dealate queens were present in only 23 of these colonies, there were 8 colonies from which the queen had apparently been

lost. At least 4 of the 30 colonies that produced no alate females were presumably incipient colonies that were still too small to produce reproductives. In addition, there were several collections (n° 13, 17, 18, 45, 59) which contained only a few adults and larvae and were probably mere colony fragments. Finally, collections N° 37 to 59 were made during the flight season; and it is probable that the alates had already flown from some of these. From the data presented in table I, it was apparent that many *H. canadensis* colonies contain a single, dealate full queen and that large numbers of alate queens are produced. These data also failed to provide any evidence for the existence of ergatoid queens. However, they did not rule out the possibility that such individuals exist, for example in the colonies or colony fragments that have no dealate queen.

A second means employed to discover whether there were any ergatoid queens involved the dissection of ergatomorphs (workerlike individuals), especially the larger ones from colonies with and without a normal queen. In addition, we dissected young ergatomorphs from colonies that produced no alate females and all intermorphs and some alate and dealate females. Tables II and III show the results of these dissections.

TABLE II. — Results of dissections of old *Harpagoxenus canadensis* workers and intermorphs.

TABELLE II. — Ergebnisse der Präparation alter Arbeiterinnen und Intermorphen von *Harpagoxenus canadensis*.

Colony No. (from table I)	Dealate queen	Brood produced	Workers (= ergatomorphs)			Intermorphs		
			dissected	with spermatheca	fertile	dissected	with spermatheca	fertile
8	—	♂♀☿	13	—	3	4	—	3
13	—	—	3	—	—	—	—	—
17	—	—	4	—	—	—	—	—
18	—	☿	3	—	—	—	—	—
21	—	—	34	—	—	1	—	—
22	—	♂	1	—	—	—	—	—
24	—	♂♀☿	42	—	5	7	—	2
25	—	♂♀☿	4	—	—	—	—	—
30	—	☿	5	—	—	—	—	—
38	—	♂ ☿	3	—	—	—	—	—
58	—	☿	9	—	—	—	—	—
59	—	—	2	—	—	—	—	—
5	1	♂♀☿	3	—	—	1	—	—
7	1	♂♀☿	3	—	—	3	—	—
10	1	♂♀☿	15	—	—	—	—	—
11	1	☿	6	—	1	—	—	—
16	1	♂ ☿	16	—	—	—	—	—
20	1	♂♀☿	10	—	4	2	—	1
23	1	♂	12	—	—	—	—	—
26	1	♂♀☿	12	—	1	3	—	—
31	1	♂♀☿	3	—	1	—	—	—
36	1	♂♀☿	3	—	1	—	—	—
22 col.			206	0	16	21	0	6

Since none of the intermorphs or workers had a spermatheca, these dissections established that none of the colonies that lacked a dealate queen had an ergatoid queen in her place. However, just as is the case in *H. sublaevis* (BUSCHINGER and WINTER, 1978), some workers that lacked a spermatheca were nonetheless fertile to a certain extent, since their ovariole contained several developing eggs and small corpora lutea. In these fertile but uninseminated individuals, the ovarioles are about as long as the total length of the gaster, *i. e.* longer than in nonfertile workers but shorter than in queens whose ovarioles may be as long as the total lenght of the body. As is the case in *H. sublaevis,* these fertile workers occur in some queen-right colonies, too. All the offspring of such individuals should be males since the eggs cannot be fertilized.

As a third means of determining whether ergatoid queens exist in *H. canadensis,* we dissected young ergatomorphs and intermorphs that eclosed in the laboratory. Table III contains the results of these dissections and of dissections of young queens that had lost their wings while still in their maternal colony.

TABLE III. — Results of dissection of young *Harpagoxenus canadensis* females, intermorphs, and workers.

TABELLE III. — Ergebnisse der Präparation junger *Harpagoxenus canadensis*-Weibchen, Intermorphen und Arbeiterinnen.

Colony No. (from table I)	Dealate queen	Brood produced	Workers (= ergatomorphs)		Intermorphs		Females	
			dissected	with spermatheca	dissected	with spermatheca	dissected	with spermatheca
8	—	♂♀☿	3	—	1	—	2	2
50	—	♂♀☿	1	—	1	—	1	1
53	—	♂♀☿	3	—	1	—	1	1
55	—	☿	1	—	1	—	3	3
61	—	♂♀☿	1	—	—	—	5	5
5	1	♂♀☿	4	—	—	—	—	—
26	1	♂♀☿	3	—	3	—	2	2
31	1	♂♀☿	5	—	—	—	—	—
36	1	♂♀☿	3	[1]	2	[2]	—	—
39	1	☿	3	—	—	—	2	2
42	1	—	1	—	—	—	—	—
48	1	♂ ☿	5	—	—	—	—	—
60	1	♂♀☿	2	—	—	—	3	2 (2)
13 col.			35	[1] (1)	9	[2] (1)	19	18

(1) In these cases the spermathecae were very small, about 1/10 the normal size, and apparently not appropriate to function normally.

(2) One normal, dealate female without spermatheca !

None of the eclosing intermorphs or ergatomorphs possessed a normally developed spermatheca. One colony (N° 36, table III) did yield two intermorphs

and one worker with very tiny receptaculum-like bladders about 1/10 the size of a normal spermatheca. On the other hand, one of the 19 dealate young females that we dissected had a normal ovary with 6 ovarioles but no receptaculum at all. Most of the other young females were newly inseminated, a fact which indicates that they had mated with males from their mother colony. From these data we conclude that true ergatoid queens that are capable of being inseminated and functioning as the principal reproductive females in colonies do note occur in *Harpagoxenus canadensis*, at least not in the populations that we sampled.

While collecting data on female polymorphism, we incidentally acquired certain other informations regarding the internal anatomy of *H. canadensis*. In table IV, we present our findings concerning the number of ovarioles in *H. canadensis* workers, queens, and intermorphs. The number of ovarioles is highly variable in workers and intermorphs. However, almost all the queens have 6 ovarioles.

TABLE IV. — Numbers of ovarioles in *H. canadensis* workers, females, and intermorphs. (For comparison the ovariole numbers of *H. sublaevis* workers are indicated.)

TABELLE IV. — Ovariolenzahl von Arbeiterinnen, Weibchen und Intermorphen von *H. canadensis*. (Zum Vergleich sind die Ovariolenzahlen von *H. sublaevis*-Arbeiterinnen angegeben.)

n ovarioles	2	3	4	5	6	7	8
Workers (224)	84	48	35	24	32	1	—
Interm. (27)	4	4	5	5	9	—	—
Females (26)	—	—	—	—	25	1	—
H. sublaevis ☿ ☿ (247)	8	7	19	34	139	34	4

As is apparent from inspection of the table, the number of ovarioles ranged from 2 to 7 in *H. canadensis* workers and intermorphs, figures which compare closely with the range of 2 to 8 in workers and intermorphs of *H. sublaevis* (BUSCHINGER and WINTER, 1978). However, while the mean number of ovarioles in *H. canadensis* workers is 3.44 ± 1.46 (S.D.), the mean number of ovarioles in 247 *H. sublaevis* workers was 5.67 ± 1.15 (S.D.). These means differ significantly ($t = 18.30$, df $= 469$, $p < .001$). However, a single colony of *H. canadensis* showed an interesting divergence from the norm of its species which approached the norm of *H. sublaevis*. Fifteen workers from colony N° 10 (table I) had a mean of 5.87 ± 0.52 (S.D.), ovarioles.

H. canadensis workers and queens have 5 Malpighian tubules, a figure identical to that in *H. sublaevis* and in the host species of the subgenus *Mychothorax*. The poison glands of *H. canadensis* and *H. sublaevis* are also about the same size. However, the Dufour's gland of *H. canadensis* is smaller than that in *H. sublaevis*. In fact, in *H. canadensis*, the Dufour's gland is only slightly larger than in the host species (fig. 2, 3 and 4).

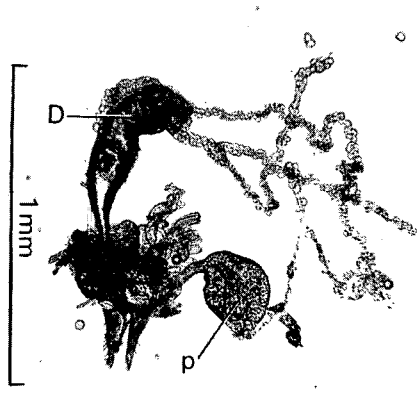

FIG. 2.

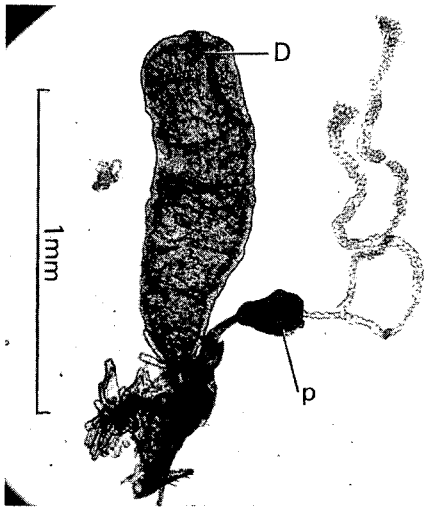

FIG. 3

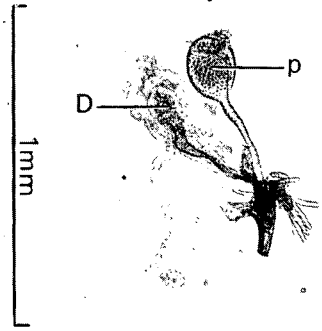

FIG. 4

FIG. 2. — Sting glands of a Harpagoxenus canadensis worker, *D* : Dufour's gland; *P* : poison gland. The tubules of the poison gland are always closely attached to the free end of the Dufour's gland.

ABB. 2. — Stacheldrüsen einer Harpagoxenus canadensis-Arbeiterin. *D* : Dufourdrüse; *P* : Giftdrüse. Die Schläuche der Giftdrüse sind immer mit dem freien Ende der Dufourdrüse verwachsen.

FIG. 3. — Sting glands of a Harpagoxenus sublaevis worker (notice the extremely large Dufour's gland ! *D* : Dufour's gland; *P* : poison gland.

ABB. 3. — Stacheldrüsen einer Harpagoxenus sublaevis-Arbeiterin (Man beachte die extrem große Dufourdrüse !) *D* : Dufourdrüse; *P* : giftdrüse.

FIG. 4. — Sting glands of a slave worker (Leptothorax sp. near L. muscorum). *D* : Dufour's gland; *P* : poison gland.

ABB. 4. — Stacheldrüsen einer Arbeiterin der Sklavenart (Leptothorax sp., L. muscorum nahestehend). *D* : Dufourdrüse; *P* : giftdrüse.

Finally, we note that *H. canadensis,* like *H. sublaevis,* is absolutely monogynous. We never found more than one fertile queen in a colony. In colonies where several young queens had been recently inseminated by their brothers (N° 60, 61 in table III), there was a lot of fighting among these individuals, fighting which caused the loss of appendages and eventually many deaths.

DISCUSSION

In contrast to *H. sublaevis, H. canadensis* appears not to have any ergatoid queens at all. The ergatoid individuals which were described by SMITH (1939), GREGG (1945), and CREIGHTON (1950) should more properly be termed « intermorphs » (BUSCHINGER and WINTER, 1975). This term is to be preferred to the older term « intercaste » since it refers exclusively to external morphology without making any reference to function. None of the intermorphs or workers that we dissected had a spermatheca. Also in contrast with the situation in *H. sublaevis,* in *H. canadensis* the spermatheca seems to be the last organ of the queen to develop during the final larval and early pupal stages. In this connection, it is interesting to note that we found one apparently normal alate female that had no spermatheca (colony N° 60, table III).

Although it is possible that true ergatoid queens may occur in other populations of *H. canadensis,* there is little reason to believe that they do. SMITH (1939) and GREGG (1945) describe the simultaneous occurrence of both full queens and ergatoid individuals in material from Quebec City, Quebec (apparently the specimens were collected outside their nest) and from Duluth, Minnesota (a single colony with a dealate queen). GREGG (1945) also mentions that R. P. GORHAM found one winged female near Kentville, Nova Scotia. Finally, R. STUART and T. ALLOWAY have each found colonies of *H. canadensis* containing single dealate queens in Moncton, New Brunswick and in Oakville and Mississauga, Ontario. Thus, full queens occur in fairly high numbers in all localities where *H. canadensis* has been collected. If ergatoid queens exist at all in *H. canadensis,* they are surely rare, perhaps as rare or even rarer than the full queens of *H. sublaevis.*

So far, we can offer no real explanation for the frequent occurrence of ergatoid queens in *H. sublaevis* or for their apparent absence in *H. canadensis.* However, it is easy to imagine that the capacity to disperse by flying is essential to the survival of *H. canadensis* in many of the localities where we have collected it. Especially near Rouyn-Noranda, Quebec, the populations of both the host species and *H. canadensis* are rather scattered and restricted to small isolated rocky hills which are surrounded and separated by extensive spruce bogs, swamps, lakes, and other areas which cannot be inhabited by these ants. On the other hand, the lack of ergatoid queens enhances the similarity between *H. canadensis* and its host species, which also have normal female polymorphism. We have already noted the lower ovariole count in *H. canadensis* which is another character in which this species resembles the host species more closely than *H sublaevis.* Moreover, laboratory observations indicate that *H. canadensis* workers forage for food and care for their brood more than workers of *H. sublaevis* (ROBIN STUART, unpublished data). Taken as a whole, these facts seem to indicate that *H. canadensis* is a somewhat less specialized slave-maker than *H. sublaevis.* However, further studies, including

studies of the Mongolian species *H. zaisanicus*, will be necessary before we can decide whether *H. canadensis* may be considered to represent an evolutionary « ancestor » of *H. sublaevis*.

Studies of the second North American species of *Harpagoxenus*, *H. americanus*, have convinced us that this species is so different from *H. canadensis* and *H. sublaevis* both behaviourally and morphologically that it shoud probably be removed from the genus *Harpagoxenus*. Numerous behavioural and certain morphological similarities seem to link *americanus* with the slave-maker *Leptothorax duloticus* and with their common host species of the subgenus *Leptothorax* in the strict sense (or subgenus *Myrafant* M. R. Smith). These findings will be presented more fully elsewhere.

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